

# A new genus and species of apoid wasps from Saxonian amber (Hymenoptera: Apoidea: Crabronidae)

Michael OHL & Daniel J. BENNETT

**Abstract:** *Palarpactophilus saxonicus* gen.n. and sp.n. is described from Middle Eocene (Lutetian) Saxonian amber from Bitterfeld, Germany. The new genus and species are diagnosed and important characters are illustrated with microphotographs. Within the Crabronidae the fossil is placed in the tribe Pemphredonini, and a possible affinity to the Spilomenina is discussed.

**Key words:** *Palarpactophilus saxonicus*, Pemphredoninae, Spilomenina, fossil, new genus, new species, taxonomy, Australasian region, Baltic amber, Saxonian amber.

**Santrauka:** *Palarpactophilus saxonicus* n.gen. ir n.sp. yra aprašomas iš vidurinio eoceno (lutetis) Saksonijos gintaro Biterfeldo vietovėje, Vokietijoje. Pateikiama naujos genties ir naujos rūšies diagnostika, o svarbūs požymiai iliustruojami mikrofotografijose. Naujas taksonas talpinamas triboje Pemphredonini, Crabronidae. Aptariami galimi ryšiai su Spilomenina.

**Raktiniai žodžiai:** *Palarpactophilus saxonicus*, Pemphredoninae, Spilomenina, fosilija, nauja gentis, nauja rūšis, taksonomija, Australazijos regionas, Baltijos gintaras, Saksonijos gintaras.

## Introduction

The apoid wasp subfamily Pemphredoninae belongs in the large and diverse clade Crabronidae (PRENTICE 1998; MELO 1999; OHL & BLEIDORN 2006). Pemphredonines are usually small or tiny, and nesting in any kind of pre-existing cavity (hollow stems and twigs in particular) is abundant in the subfamily. In such nests they typically provide their progeny with auchenorrhynchan or sternorrhynchan Hemiptera, but other small insects such as thrips and collembolans are also attacked by a few members (BOHART & MENKE 1976).

The pemphredonine subtribe Spilomenina comprises about 160 species in four genera, namely *Arpactophilus*, *Microstigmus*, *Spilomena*, and *Xysma*. This subtribe is remarkable among Apoidea for two aspects: at least some species of *Arpactophilus* and *Microstigmus* exhibit a high level of social behavior (e.g., MATTHEWS 1991; MATTHEWS & NAUMANN 1989), which rarely occurs in the otherwise usually solitary apoid wasps. The other aspect is the remarkable diversity of recent species, best exemplified by *Arpactophilus*, which has been progressively revealed by a number of revisionary studies. MENKE (1989) pointed out that *Arpactophilus* has apparently “exploded”, evolutionarily speaking in the Australasian region“ and that there exist at least 40 species from Australia alone. He has also seen unde-

scribed species from New Guinea, New Britain, the Solomon Islands, New Caledonia and Fiji. BOHART (1999) described 17 new species from New Caledonia. In the Australian National Insect Collection, Canberra, specimens of *Arpactophilus* have been sorted into more than 60 morpho-species (NAUMANN unpubl., cited in MATTHEWS & NAUMANN 2002), and nine of them have been described by MATTHEWS & NAUMANN (2002). In total, 43 species of *Arpactophilus* have been formally described as yet (PULAWSKI 2008). In 2005, one of us (MO) received 79 individuals of *Arpactophilus* from New Caledonia sent by the Queensland Museum for identification. These have been sorted to 24 provisional species, 20 of which cannot be reliably identified with BOHART’s (1999) key to New Caledonian *Arpactophilus* and probably represent undescribed species (JAENICKE & OHL, unpubl. data). The high morphological and taxonomical diversity on New Caledonia implies a high level of island endemism, and based on the published and unpublished records, the Recent species diversity of *Arpactophilus* certainly exceeds the currently known number of species considerably.

Among Saxonian amber inclusions from the Museum für Naturkunde in Berlin we recently discovered an apoid wasp that readily keyed out to *Arpactophilus* with the key to genera in BOHART & MENKE (1976). Although the specimen clearly shows affinities to

*Arpactophilus* and the Spilomenina, it shows a number of significant differences to Recent species. Thus, the purpose of this paper is to describe *Palarpactophilus saxonicus* gen.n. and sp.n. and to discuss its affinities to the Spilomenina.

The age of Saxonian amber has been subject to controversial discussions. WEITSCHAT (1997) convincingly demonstrated that Saxonian amber is merely redeposited Baltic amber and, thus, of Middle Eocene age (see also ENGEL 2001). This led BENNETT & ENGEL (2006) to list the pemphredonine wasp *Passaloecus munax* SORG (originally described from Saxonian amber) as originating from Baltic amber. Although this is correct in terms of the mere age of the resin, the relevant information (that Saxonian amber is not true Baltic amber but redeposited Baltic amber) would have been obscured had they not further discussed this nomenclatural problem. Although Baltic and Saxonian ambers are identical in terms of their geological origin, we prefer to use Saxonian amber for the amber from Bitterfeld, Saxony to emphasize its specific geological history and geographic origin, in contrast to true Baltic amber.

## Systematic Paleontology

### *Palarpactophilus* OHL & BENNETT, gen.n.

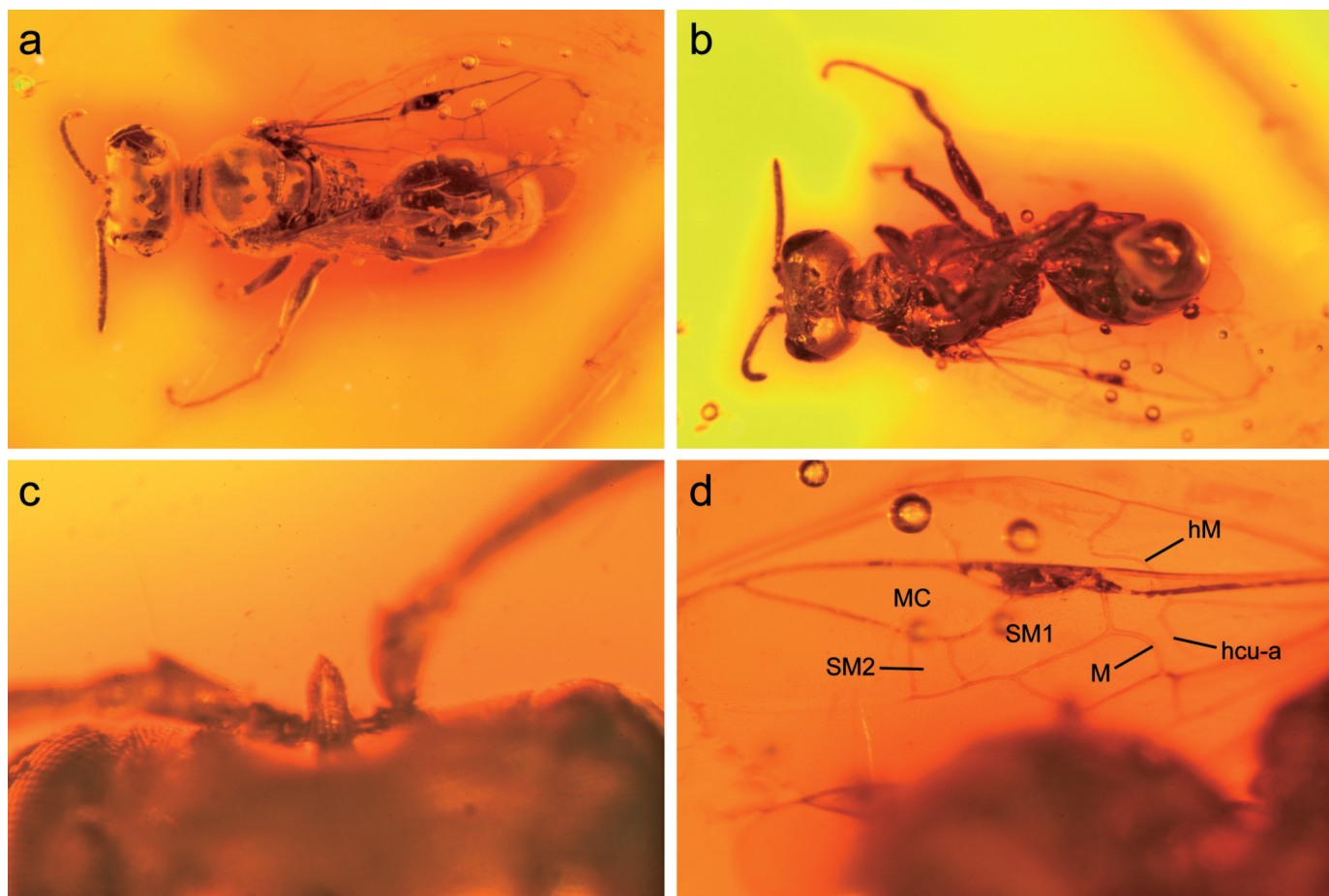
**Type species:** *Palarpactophilus saxonicus* OHL & BENNETT, sp.n.

**Diagnosis:** *Palarpactophilus* is here classified with reference to BOHART & MENKE (1976), MENKE (1989), and PRENTICE (1998) but follows the latter two with regards to subtribal categories. The fossil is recognized as belonging to the Pemphredoninae by the combination of its small size, cuboidal head, normal ocelli, sub-parallel inner orbits, simple mandible exteroventrally, and single midtibial spur. Of the two pemphredonine tribes it is recognized as belonging to the Pemphredonini by the two submarginal cells (three in Psenini, two or fewer in Pemphredonini); toruli positioned against the frontoclypeal sulcus; mandibles bidentate apically; and low, broad pronotal collar. *Palarpactophilus* is excluded from all subtribes of the Pemphredonini as represented by modern taxa as follows: from Pemphredonina by its two discoidal cells (as opposed to three), hind wing medial cell not extended much beyond origin of radial sector, and without facial fovea extended onto frontal area (however, the relative size of the marginal cell to the pterostigma is arguably more like this subtribe in the fossil than the others); from Ammoplanina by the orthognathous head (rather than prognathous), longer marginal cell, presence of an acetabular carina, and less-reduced fore and hind wing venations; from Stigmina by the lack of both a long maxillary palpus and long peti-

ole; from Spilomenina by its six-segmented maxillary palpus (rather than five) and strong mesopleural sulcus; and from Spilomenina other than *Arpactophilus* by the presence of an occipital carina. The fossil and *Arpactophilus* also share a very short petiole, short first segment of maxillary palpus, forewing with elongate, closed marginal cell (Fig. 1d), and hind wing media diverging before cu-a (Fig. 1d). In addition to the number of palpal segments, *Palarpactophilus* differs from *Arpactophilus* in that the occipital carina in *Palarpactophilus* is in close contact to the hypostomal carina (Fig. 2a) (as opposed to its position considerably behind the oral fossa in even the putatively most plesiomorphic species of *Arpactophilus*) and in that the forewing basal veinlet of discoidal cell I (a section of M) is markedly bent, forming an angle between 90° and 120° (veinlet straight or indistinctly bent, angle 180° or slightly less in *Arpactophilus*) (Fig. 1d).

**Etymology:** The name is a combination of the prefix pal-, which refers to the Greek palaiós, meaning ancient, and *Arpactophilus*, a close relative of the new genus. The name is masculine.

**Remarks:** Despite the differences of *Palarpactophilus* to the pemphredonine subtribes noted above, the body of evidence suggests an affinity to Spilomenina, possibly as a stem-group to the subtribe or to *Arpactophilus* only. The morphology of *Arpactophilus* is remarkably diverse and character-rich, and this includes a significant diversity of integument sculpture, clypeal and labral dentition, and general body shape. An interesting character in *Arpactophilus*, which is not diagnostic for the genus, is the frontal line between frontoclypeal sulcus and midocellus, which is usually raised to an elevated carina (interantennal carina sensu BOHART & MENKE 1976). MENKE (1989) pointed out that in some species that lack coarse sculpture, the frontal carina might be fine, but it is discrete in any case. In many described and undescribed species of *Arpactophilus*, the frontal carina is markedly raised into significant lamellae or other elaborate facial features. The newly discovered fossil also has the frontal carina raised into a significant thorn-like structure between the antennal sockets. This and the other characters listed above, as well as the general body shape, suggest an association with *Arpactophilus*. Hence, it is tempting to interpret the fossil as a rather plesiomorphic, that is, basal species in *Arpactophilus*. However, if the reduced palpal formula 5-4 is really a synapomorphic trait of *Arpactophilus*, *Spilomena*, *Xysma*, and *Microstigmus* as proposed by MENKE (1989) and PRENTICE (1998), it was likely present in the stem species of *Arpactophilus* as well. If this interpretation is true, placement of the fossil in *Arpactophilus* is contradictory. Additionally, *Spilomena*, *Xysma*, and *Microstigmus* lack an occipital carina and a raised frontal carina and have an



**Fig. 1:** *Palarpactophilus saxonicus* sp.n., holotype. (a) dorsal view; (b) ventral view; (c) midfrontal process in dorsal view; (d) right fore and hind wing in ventral view. Abbreviations: M = abscissa of media, the basal veinlet of discoidal cell I; MC = marginal cell; SM 1 and SM 2 = submarginal cell I and II; hcu-a = hind wing crossvein cu-a; hM = hind wing media.

indistinguishable point of divergence of the hind wing media from Cu. Thus, the fossil is clearly not more closely related to any of these genera. Even though the exact phylogenetic position of the new fossil cannot be absolutely assured yet, placement in a new genus as a consequence of its unique combination of characters is logically consistent with the several possibilities, i.e. as the stem group to Spilomenina, *Arpactophilus* only, or further removed from Spilomenina altogether.

### ***Palarpactophilus saxonicus* OHL & BENNETT, sp.n. (Figs 1-2)**

**Diagnosis:** As for the genus (vide supra). However, if paralleled with the enormous diversity in *Arpactophilus*, it can be expected that other characters of the fossil are also of specific value. Candidates are: head and thoracic dorsum microsculptured, without ridges or punctures (Fig. 2b); most mesopleural sulci coarsely pitted (Fig. 2c); with a peg-like process between antennal sockets in a deeply impressed scapal basin (Fig. 1c); propodeal dorsum coarsely areolate (Fig. 2d); and tergite VI narrowly truncate apically.

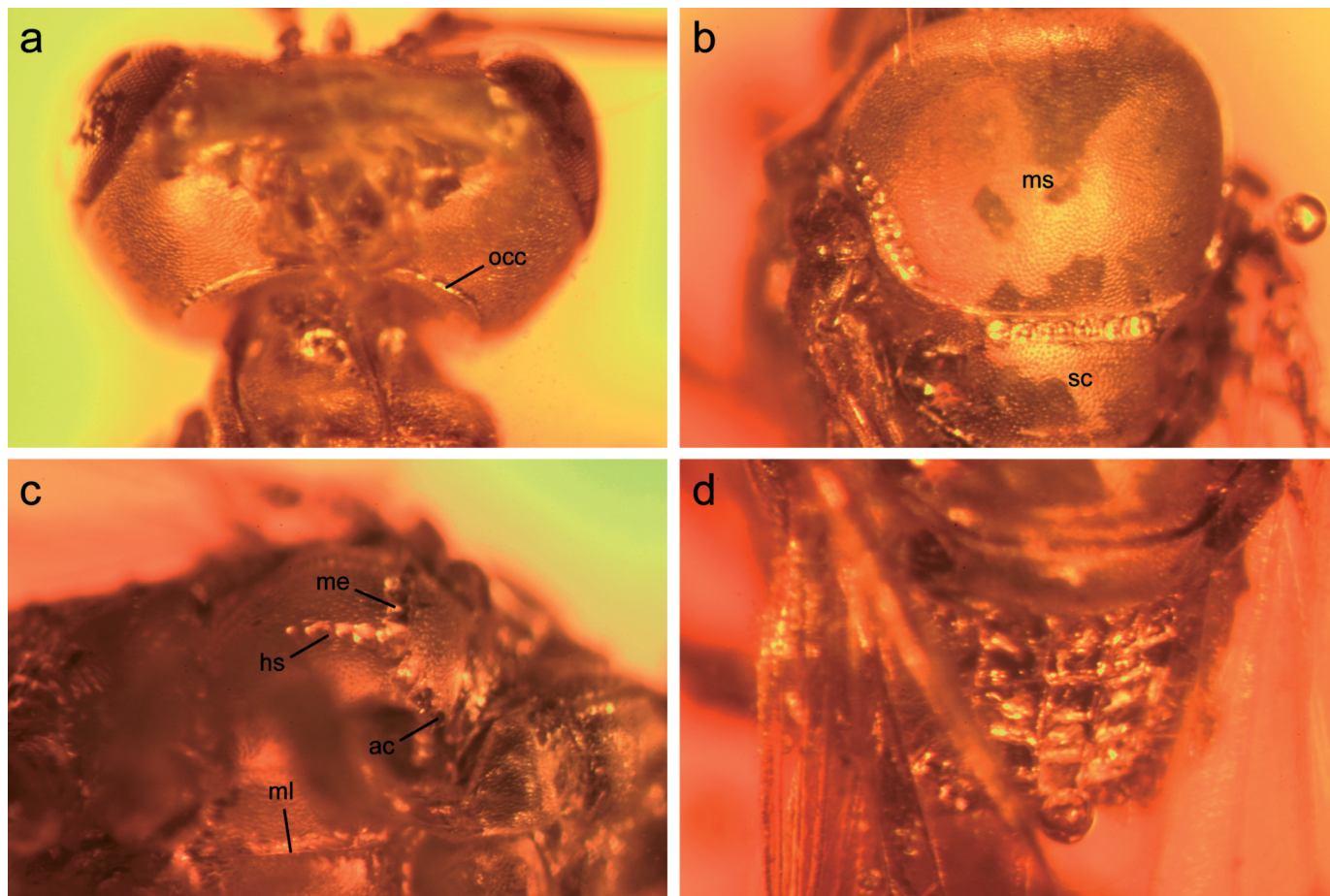
**Holotype:** ♀. Saxonian amber [redeposited Baltic amber; Lutetian stage, middle Eocene], labeled "Serie 10", Bitterfeld, Germany (Museum für Naturkunde, Berlin, paleontological collection; MB.I.5438). Preserved in a clean, polished, irregularly oval piece of amber (size about 17 x 15 x 4 mm).

**Description:** Based on the holotype, ♀.

Body length (without appendages) 3.9 mm; forewing length 2.7 mm; head width 1.1 mm.

Head: Orthognathous; face rather rounded in frontal view, not elongate; integument microsculptured throughout; eyes slightly diverging below; ocular-ocular distance 1.2x midocellar diameter (Fig. 1a); scapal basin depressed, dorsal margin probably carinate; with peg-like process between antennal sockets, almost perpendicular to scapal basin, process about as long as twice maximum scapal width, parallel-sided in basal two-thirds, sharply pointed apically (Fig. 1c); scape dorsally extending beyond scapal basin; flagellomeres about as wide as long, terminal flagellomeres twice as long as wide, tapering apically; mandible with two subequal apical teeth;





**Fig. 2:** *Palarpactophilus saxonicus* sp.n., holotype. (a) head ventrally; (b) mesoscutum and scutellum in dorsal view; (c) right mesopleuron in oblique ventral view; (d) propodeal dorsum. Abbreviations: ac = acetabular carina; hs = hypersternaulus; me = mesepisternal sulcus; ml = midventral line; ms = mesoscutum; occ = occipital carina; sc = scutellum.

labrum not protruding, apex shallowly emarginate; palpal formula 6-4, basal segment of maxillary palpus very short, segments 2-3 slightly broadened, segments 4-6 elongate; gena behind eye narrow, not more than one-third eye width; malar space absent; occipital carina a complete circle, subcontiguous with hypostomal carina (Fig. 2a).

Mesosoma: Thoracic dorsum microsculptured except for coarsely pitted grooves along anterior scutellar and posterolateral scutal margins (Fig. 2b); pronotum short, with a low, transverse carina dorsally; propleuron with pair of shiny impressions anteroventrally; ventral angle of pronotum with transverse rugulae; mesopleuron with postspiracular groove, mesepisternal sulcus, acetabular sulcus, scrobal sulcus, and hypersternaulus (Fig. 1c); all mesopleural sulci coarsely pitted, postspiracular groove and scrobal sulcus less so; midventral line flanked by shallowly pitted grooves; precoxal groove coarsely pitted; metapostnotum (= propodeal dorsum) coarsely areolate (Fig. 2d), carina in posterolateral angle raised to form low lamella; hindtibia with a few bristles; forewing (Fig. 1d) with two submarginal cells, the sec-

ond being much smaller; marginal cell closed, very long and broad basally; pterostigma large, but significantly smaller than marginal cell; section of M at discoidal cell I (= basal veinlet of discoidal cell I) markedly bent at an angle of 90°-120°; hind wing media diverging before cu-a (Fig. 1d).

Metasoma: petiole present but indistinct; tergites microsculptured; tergite VI narrowly truncate at apex, pygidial plate absent.

## Discussion

Spilomenina is essentially worldwide in distribution; *Spilomena* is widespread, *Xysma* is known from the New World and South Africa, *Microstigmus* is Neotropical, and *Arpactophilus* is Australasian, as has been more fully noted above (BOHART & MENKE 1976; PULAWSKI 2008). The locality of *Palarpactophilus* combined with its similarities to *Arpactophilus* make an interpretation in which these taxa together comprise a clade within the Spilomenina that underwent extinction in the northern hemisphere a tempting argument. This may

very well be the case. However, based on the plesiomorphic number of labial palp segments, it seems more likely (as discussed above) that *Palarpactophilus* is the sister group to all other Spilomenina or further removed from the subtribe, in which case such a conclusion is not necessarily warranted.

The small body size and nesting habits of Pemphredoninae make them good candidates to be preserved in fossil resin. Indeed, most apoid wasps known from amber deposits belong in the Pemphredoninae (ANTROPOV 2000a, b; BENNETT & ENGEL 2006), this despite being outnumbered in the modern fauna by the Bembicinae, Philanthinae, and, by about four and a half times, the Crabroninae (PULAWSKI 2008). Five species from Baltic amber have been described in a modern genus, *Passaloecus*, by SORG (1986) and BUDRYS (1993), and 15 more species from various amber deposits have been placed in 11 extinct genera (BUDRYS 1993; ANTROPOV 2000a, b; EVANS 1969, 1973). The antiquity of the Pemphredonini is solidly indicated by the Cretaceous fossils *Psolime-na electra* ANTROPOV (2000a), *Prolemistus apiformis* ANTROPOV (2000b), and *Lisponema singularis* EVANS (1969). Whether or not Spilomenina or the other pemphredonine subtribes are as ancient is debatable owing to the ambiguity of the subtribal status of these fossils. EVANS (1969) regarded *Lisponema* as near the genus *Spilomena* because of their highly similar wing venations and body forms. Additionally, the sessile abdomen is consistent with placement in Spilomenina, though this character occurs elsewhere in the Pemphredonini. However, ANTROPOV (2000a) cast doubt on the phylogenetic position of *Lisponema*, arguing that its missing head leaves too many important characteristics unknown to place the fossil within the Spilomenina or in any pemphredonine subtribe. *Palarpactophilus* represents yet an additional pemphredonine genus with uncertain phylogenetic affinities. A phylogenetic analysis of the Pemphredoninae which takes into account the numerous fossil taxa is needed and might well clarify these ambiguities, providing insight into the age, diversification, and subsequent extinction of pemphredonine taxa.

## Zusammenfassung

*Palarpactophilus saxonicus* gen.n. und sp.n. aus dem Sächsischen Bernstein von Bitterfeld wird beschrieben. Sächsischer Bernstein wird als umgelagerter Baltischer Bernstein angesehen, so dass das Alter des Sächsischen Bernsteins als Mittleres Eozän angenommen werden kann. Die neue Gattung und neue Art werden gekennzeichnet, und wesentliche Merkmale werden in Mikrofotografien dargestellt. Die Position von *Palarpactophilus saxonicus* innerhalb der Pemphredoninae wird kritisch diskutiert.

## Acknowledgements

We are grateful to Dr. Christian NEUMANN, Museum für Naturkunde, Berlin, Germany, for permitting us to sort through all the Saxonian amber specimens and to study some of them in more details. We are indebted to Dr. Christopher BURWELL, Queensland Museum, Brisbane, Australia, for borrowing large numbers of *Arpactophilus* from New Caledonia to MO. The participation of DJB was supported by U.S. National Science Foundation grant EF-0341724 to M.S. ENGEL (HymA-ToL: Hymenoptera Tree of Life).

## Literature

- ANTROPOV A.V. (2000a): A new digger wasp (Hymenoptera, Sphecidae, Pemphredoninae) from New Jersey amber. — In: GRIMALDI D. (Ed.), *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*. Backhuys Publishers, Leiden: 339-343.
- ANTROPOV A.V. (2000b): Digger wasps (Hymenoptera, Sphecidae) in Burmese amber. *Bull. Nat. Hist. Mus. London (Geol. Ser.)* **56**: 59-77.
- BENNETT D.J. & M.S. ENGEL (2006): A new moustache wasp in Dominican amber, with an account of apoid wasp evolution emphasizing Crabroninae (Hymenoptera: Crabronidae). — *American Mus. Nov.* **3529**: 1-10.
- BOHART R.M. (1999): New species of *Arpactophilus* from the island of New Caledonia (Hymenoptera, Sphecidae). — *Insecta Mundi* **13**: 97-110.
- BOHART R.M. & A.S. MENKE (1976): *Sphecids Wasps of the World: A Generic Revision* — University of California, Berkeley.
- BUDRYS E.R. (1993): Digger wasps of the subfamily Pemphredoninae (Hymenoptera, Sphecidae) from the Baltic and Taimyr amber. — *Acta Entomol. Lituanica* **2**: 34-56.
- ENGEL M.S. (2001): A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). — *Bull. American Mus. Nat. Hist.* **259**: 1-192.
- EVANS H.E. (1969): Three new Cretaceous aculeate wasps (Hymenoptera). — *Psyche* **76**: 251-261.
- EVANS H.E. (1973): Cretaceous aculeate wasps from Taimyr, Siberia (Hymenoptera). — *Psyche* **80**: 166-178.
- MATTHEWS R.W. (1991): Evolution of social behavior in sphecids wasps. — In: ROSS K.C. & R.W. MATTHEWS (Eds), *The Social Biology of Wasps*. Comstock Publishing Associates, Ithaca and London: 570-602.
- MATTHEWS R.W. & I.D. NAUMANN (1989): Nesting biology and taxonomy of *Arpactophilus mimi*, a new species of social sphecids (Hymenoptera: Sphecidae) from Northern Australia. — *Australian J. Zool.* **36**: 585-597.
- MATTHEWS R.W. & I.D. NAUMANN (2002): Descriptions and biology of nine new species of *Arpactophilus* (Hymenoptera: Crabronidae), with a key to described Australian species. — *J. Hym. Res.* **11**: 101-133.
- MELO G.A.R. (1999): Phylogenetic relationships and classification of the major lineages of Apoidea (Hymenoptera), with emphasis on the crabronid wasps. — *Sci. Pap. Nat. Hist. Mus., Univ. Kansas* **14**: 1-55.

- MENKE A.S. (1989): *Arpactophilus* reassessed, with three bizarre new species from New Guinea (Hymenoptera: Sphecidae: Pemphredoninae). — Invertebr. Tax. **2**: 737-747.
- OHL M., & C. BLEIDORN (2006): The phylogenetic position of the enigmatic family Heterogynaidae based on molecular data, with description of a new, nocturnal species (Hymenoptera: Apoidea). — Syst. Ent. **31**:321-337.
- PRENTICE M.A. (1998): The comparative morphology and phylogeny of apoid wasps (Hymenoptera: Apoidea). — Dissertation Thesis. University of California, Berkeley.
- PULAWSKI W.J. (2008): Catalog of Sphecidae sensu lato. — Internet catalog available at [http://research.calacademy.org/research/entomology/Entomology\\_Resources/Hymenoptera/sphecidae/Genera\\_and\\_species\\_PDF/introduction.htm](http://research.calacademy.org/research/entomology/Entomology_Resources/Hymenoptera/sphecidae/Genera_and_species_PDF/introduction.htm) (internet link valid as of 26 September 2008).
- SORG M. (1986): Grabwespen der Gattung *Passaloecus* aus fossilen Harzen (Hymenoptera, Sphecoidea, Pemphredoninae). *Passaloecus microceras* n.sp., Baltischer Bernstein, oberes Eozän. *Passaloecus munax* n.sp., Bitterfelder Bernstein, unteres Miozän. — Paläont. Z. **60**: 277-284.
- WEITSCHAT W. (1997): Bitterfelder Bernstein – Ein eozäner Bernstein auf miozäner Lagerstätte. — Metalla **66**: 71-84.

#### Address of authors:

Michael OHL

Leibniz-Institut für Evolutions- und Biodiversitäts-  
forschung an der Humboldt-Universität zu Berlin  
Museum für Naturkunde, Sektion Entomologie  
Invalidenstr. 43  
10115 Berlin, Germany  
E-Mail: [michael.ohl@museum.hu-berlin.de](mailto:michael.ohl@museum.hu-berlin.de)

Daniel J. BENNETT

Division of Entomology, Natural History Museum, and  
Department of Ecology & Evolutionary Biology  
University of Kansas  
1501 Crestline Drive, Suite 140  
Lawrence Kansas 66049-2811, USA  
E-Mail: [danben@ku.edu](mailto:danben@ku.edu)